III. *On the Breeding-habits of some West-African Fishes, with an Account of the External Features in Development of* Protopterus annectens, *and a Description of the Larva of* Polypterus lapradei. *By* J. S. Budgett, *M.A., F.Z.S., Trinity College, Cambridge.*

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[Plates X. & XI. and text-figures 19–23.]

Contents.

I.—Introduction.

The months of June, July, and August of this year I spent on M'Carthy Island, in the river Gambia, hunting for the eggs of *Polypterus.* But in this paper I have recorded not only the result of my work in this direction, but also my observations upon the breeding-habits of the African Lung-fish, *Protopterus annectens*, of the Teleosteans *Gymnarchus niloticus*, *Heterotis niloticus*, and *Sarcodaces odoë*, and also my observations upon the nests of another Teleostean, presumably *Hyperopisus bebe.* Towards the expenses of this expedition I received contributions from the Government Grant, from this Society, and from the Cambridge University Balfour Fund. I should here like to express my gratefulness for this assistance, which enabled me to undertake what turned out to be, so far as I was concerned, an intensely interesting collecting trip. When my results are completed, the expenditure will, I hope, be found to have been justified.

The Island of M'Carthy is six miles long and about one mile wide, and is situated 160 miles up the river Gambia. The whole of the island is low-lying, and the greater part, in the wet season, is completely under water. On the highest part of the island is the native town of Ginginberri, and the ruins of the old military settlement where I lived. The eastern half of the island is partly under cultivation, and here the natives plant rice on the low land, and kuskus or millet on the high land. The western half of the island is little cultivated, and here was my hunting-ground.

The whole island is traversed by one main swamp, which has the appearance of having been at one time an old bed of the river, and which is seldom quite dry, even in the dry season. Parallel with this lie several shallower and more irregular swamps, all of which become perfectly dry in the dry season. These swamps are separated by belts of low forest, composed largely of leguminous trees, palms, and fig-trees. The swamps themselves are mostly choked with papyrus and other swamp-grasses; while in the middle there is often a little open water covered with several kinds of lovely water-lilies.

The amount of open water depends largely on the rapidity of the oncoming of the rains. In the present season there was little open water, as the rains came on very slowly and gave the grass time to grow abundantly.

As the rainy season advances the swamps become filled with water, the river rises and soon becomes connected with the swamps by narrow creeks, up which great numbers of fishes pass to the flooded grasslands to spawn. Conspicuous amongst these are the two species of *Polypterus*—*P. lapradei* Steind. and *P. senegalus* Cuv.

II.—Results of the Search for *Polypterus* Eggs.

From what I observed in my former expedition of its habits, I concluded that the eggs of *Polypterus* might be obtained by one of three methods:—

(1) Hunting the flooded grasslands for the eggs in a state of nature.

(2) Inducing *Polypterus* to breed in captivity.

(3) Artificially fertilizing the eggs of the female.

The first method was persistently tried without success, especially on the occasion of spawning females being brought in, when, taking a number of natives to the spot, we examined every foot of water within a hundred yards of the place where the female had been caught. Five spawning females were caught, but in no case did I find a single egg.

For the purpose of the second method I took out to the Gambia with me a large number of wire hurdles, with which I made four enclosures in the swamp. During the second half of June about fifty *Polypteri* were caught in pools by the river-side. As the rains had scarcely begun, and consequently there was no water as yet on the land where I had made my enclosures, I temporarily turned my fish into large floating cages in the river, and fed them regularly on minced meat. A few days after turning them in, I came one evening to feed them, and found that the two cages had been torn to pieces by crocodiles and the fishes had escaped. I then rigged up some temporary cages in pools by the river-side, into which I turned six pairs of *P. lapradei* and fifteen pairs of *P. senegalus*. By the 30th of July there was sufficient water in my swamp-enclosures to turn in the fishes, and there they seemed quite happy, as the grass was now two feet high and I fed them regularly every night. The enclosures were each eighteen feet long and six feet wide. As soon as I put the food into the water at one end of the enclosure the *P. senegali* came hurrying through the grass from all parts, and greedily devoured it without the least appearance of shyness. The *P. lapradei*, however, were considerably more shy, and continually damaged themselves against the wire netting. Thus the *Polypteri* remained until the 5th of September, and though I examined every inch of the enclosure every other day, I found no traces of eggs.

The third method was not tried so frequently as I could have wished, as I could not obtain anything like the number of *Polypteri* that I procured in the previous season. The natives at this time use a kind of basket for catching fishes, which is called the "wusungu." This they deftly drop over the fishes as they see them move in the grasses, and putting their hand into the basket from above, draw forth the captives. Whereas by this method I obtained an abundant supply of *Polypterus* last year at the price of sixpence apiece, this year I raised the price to two shillings apiece and was yet unable to get any large number of specimens.

The first spawning female was brought to me on the 3rd of July. It was a *Polypterus senegalus*, and, on holding it up by the head, it extruded successively twelve eggs. I had two males with which I tried to fertilize these eggs. One by one I tried them: first by placing them on the anal fin and on the vent of the male, then by mixing them with the fluid obtained from the seminal duct, and lastly by mixing them with fluid obtained from the minced testis. These eggs were then transferred to muslin stretched on a frame and placed in a large quantity of river-water. They soon attached themselves to the muslin, but though I watched them until late into the night, no further change took place and they one by one decomposed. On cutting open the female I found to my disappointment that there were no free eggs in the body-cavity, but that they were all attached to the ovary by their follicles.

The next spawning female was obtained on July 19th, when a fisherman brought me a female *Polypterus lapradei* which had two eggs in the oviduct and practically none in the ovary. There were no free eggs in the body-cavity.

On August the 9th a female *P. lapradei* was brought which had evidently spawned some time ago.

On August the 14th a female was brought which had nearly finished spawning. There were, however, no free eggs in the body-cavity. I tried to force out the eggs from the ovary, and in this manner several came away fairly easily, and I made every effort to fertilize them, but again without success.

On August the 15th another female *Polypterus* was brought, which had shed all its eggs.

In each case I took several natives to the spot where the female had been caught and made a very thorough search for the eggs in the neighbourhood, examining every blade of grass, but found not a single egg.

On August the 19th a small boy brought me a specimen of *Polypterus lapradei* only one inch and a quarter in length; it was a most beautiful object (Pl. XI. fig. 1). The upper surface is marked with black stripes on a golden ground, a conspicuous golden stripe runs on each side above the eye, across the spiracle, and along the dorsal surface of the external gill [1]. The external gills are at this stage of great size, reaching halfway to the tail, blood-red, and with a row of branches on either side. Each branch bears a row of pinnules on either side; the pinnules have the same structure as those of most Amphibian and Dipnoan external gill-filaments, being merely a long drawn-out blood-capillary loop. The afferent limb of the loop arises from the afferent artery of the gill-branch; the efferent limb of the loop joins the efferent artery of the gill-branch. Similarly the afferent artery of the gill-branch arises from the afferent artery of the external gill, while the efferent artery of the gill-branch joins the efferent artery of the external gill. Every alternate gill-branch is much smaller than the next gill-branch (Pl. XI. fig. 2). Each of these small gill-branches bends towards the surface of the body, while the large gill-branches extend parallel with the body. Thus space is economised, and the result is the same as four rows of branches on the external gill. Arising immediately behind the spiracle, the external gills may droop ventralwards posteriorly, and do not seem to be moved much by muscles, except just to straighten the shaft from the drooping position. The heart and blood-supply to the external gills can be seen with wonderful distinctness through the transparent ventral body-wall. The dorsal finlets are not differentiated from the tail, of which they seem to be only a forward prolongation. They are not distinct from one another, but form rather a continuous dorsal fin. The body is distinctly more truncate in the larva than in the adult, the head and tail-region being large. The eye is also very large in proportion.

The area of pigment ceases abruptly ventralwards in a line running from the tubular nasal opening under the eye dorsal to the shaft of the pectoral fin, thence to the base of the anal fin.

The larva was extraordinarily active, and, during the moments when it was at rest, supported the weight of its body on its pectoral fins, the blade of the fin being turned forwards and not backwards as is usually the case in the adult. The shape of the pectoral fin differs considerably from that of the adult. The ventral or postaxial border

[1] The young larva which I have described is about one third of the length of any larval Crossopterygian which has, up to the present time, been obtained. The anatomy of this specimen I hope to describe in a future paper.

of the basal lobe is in this young larva much longer than the dorsal or preaxial border; while the fin-rays become successively longer in passing from the preaxial to the postaxial border. It follows that the shape of the fin is triangular, the apex being at the extremity of the postaxial border (Pl. XI. fig. 1).

Though the spot where this larva was caught was carefully searched, I did not succeed in capturing another.

Later on the same day, the 19th of August, I had another female *P. lavradei*, which must have finished laying its eggs some weeks before.

On the 21st of August, in my own fish-trap at the mouth of the small creek which led from the river to the swamp, I found a female *P. lapradei* which had finished laying its eggs, and it looked as though, in this case, it had spawned in the river or else at the mouth of the creek. I am inclined to believe, however, that it had temporarily returned to the river side of the trap after depositing its eggs in the swamp.

On this same day I had a *Polypterus senegalus*, still crammed with eggs, but not one free egg in the body-cavity.

During the last week in August and the first in September, I killed fifteen of my captive females; but in no case could I attempt artificial fertilization, as the ova would not come away from the ovaries, and in more than one case there were signs of degeneration.

On the 5th of September I left for England, leaving five pairs of *P. senegalus* in charge of a native, who was to preserve eggs for me if any should be laid.

Though I have little success in this direction to report, I have thought it well to put on record the difficulties which I encountered in the search for the eggs of *Polypterus* in order that any future investigator who may attempt to obtain developmental material of this fish may in being forewarned be also forearmed.

The main difficulties in obtaining the eggs seem to lie in the fact that *Polypterus* probably makes no nest, and certainly lays but few eggs at a time, these being scattered, probably broadcast, throughout the thick vegetation of the flooded grass-lands. The eggs are minute, and therefore the chances of finding them in a state of nature are small in the extreme.

III.—The Habits and Life-history of *Protopterus*.

a. *Nesting-habits.*

Although the development of *Polypterus* had been the chief aim and object of my second journey to the Gambia, I was also very anxious to obtain a series of the eggs and embryos of *Protopterus*. When I was on the Gambia the previous year, I had brought me a number of eggs of *Protopterus*, but I suspected that the way in which the native told me that they had been laid was quite abnormal or altogether untrue.

I had expected, in wading about the swamps, to come across deep holes in the ground similar to the nests of *Lepidosiren*, which I had become familiar with when in the

Gran Chaco of Paraguay some three years ago with Mr. Graham Kerr. However, I never found such holes, and was completely at a loss to know where to look for the nests of *Protopterus*, the natives being entirely ignorant of any but the most obvious facts of natural history, and having declared to me that the "Cambona," as they called *Protopterus*, was viviparous.

One day my head fisherman, Sory, came to me in a great state of excitement to say that he had found the children of the Cambona. It was scorching mid-day in the height of the rainy season, the temperature 99° in the shade. After crossing one deep swamp we came to the edge of another swamp, and there, about ten yards from the water's edge, on dry ground, was an oval-shaped hole filled with water, and in the water was a great commotion (text-fig. 19); the surface of the water was being continually lashed from side to side by the tail of a Cambona, the head of which was away down under the ground. On being startled, the Cambona disappeared downwards, and the fisherman, putting his hand into the hole, drew forth a handful of larval *Protopteri*.

Text-fig. 19.

Nest of *Protopterus*.

Having now learned where to look for the nests of *Protopterus*, in a few days I found a number of similar nests, but never so far away from the water as the first one, which was found at the end of a period of drought, very unusual at this time of year. I soon found a nest full of newly-laid eggs which must have numbered several thousands, for from the first day to the day the larvæ left the nest, twenty days later, I took fifty per day for preservation without perceptibly diminishing the numbers in the nest.

Throughout the period of the larvæ being in the nest, the male *Protopterus* stays with them and guards them jealously, severely biting the incautious intruder. On one occasion the male was observed to leave the nest and to come out by a small opening which had hitherto been unnoticed, and wriggle off down to the water. This exit was always found about two feet from the main opening. Frequently there was a kind of pathway up to the entrance, where the grasses were bent aside. The main opening measured four to ten inches in diameter, while the exit rarely measured more than three inches. The depth of the nest was usually about a foot, and the shape of the nest was quite irregular. There was never any lining, and the eggs were laid on bare mud. All the males found in the nests measured about eighteen inches in length.

b. *Development of the Embryo.*

The eggs, which measure 3·5–4 mm. in diameter, begin to hatch about the eighth day, and by the tenth day the larvæ are all attached by their suckers to the side of the nest. The main features in development are remarkably like those of *Lepidosiren* lately described by Kerr, the larvæ being provided with a ventral sucker and four pairs of plumose external gills, one to each branchial arch. I have figured a few stages of the external features in development, most of which were drawn on the spot from life, in order that a comparison may be made with Kerr's excellent illustrations in the Phil. Trans. vol. 192, plates 8–12.

As all my specimens were procured from the same nest at twenty-four hours' interval, I am able to show the advancement made daily. As Kerr's material was obtained from a large number of nests, he was unable to say what was the age of each successive stage figured. Though in one nest were found a few specimens at least half a day in advancement of the rest, and a few also at least half a day behind the rest, yet the majority appeared to be at a uniform stage of development. When kept in shallow dishes I found that the development was much retarded.

Comparing Pl. X. fig. 1 with the corresponding stage in *Lepidosiren* (*op. cit.* plate 8. fig. 7*a*, 7*s*, & 7*b*), it is noteworthy that the egg is here divided into segments, which are more distinct from one another, the outer surfaces being rounder and not assuming the same curvature as the egg-capsule. In this the egg of *Protopterus* approaches the conditions of *Ceratodus*. This is the first stage of my series, so that I am not able to speak with regard to the appearance of the egg in the earliest stage of segmentation.

The subsequent down-growth of the epiblast over the invaginating yolk (as shown in Pl. X. figs. 2, 3, 4, & 5) is remarkably similar to the same process in *Lepidosiren* (*op. cit.* plate 8. figs. 10–14), the invaginating rim remaining a nearly straight line. This appears to me to be the more frequent method of invagination. Mr. Kerr has himself, however, pointed out to me that the variations which frequently occur in

Protopterus are very interesting. The invaginating rim is often curved, as in fig. 3 *a*, rather than straight, as in fig. 3, while later the invaginating rim may become somewhat V-shaped, recalling a similar appearance in certain Amphibia. The invagination culminates in a crescentic blastopore. The yolk from the earliest stage onwards in *Protopterus* is light green in colour. During segmentation the epiblastic pole of the egg is pink, and this colour gradually replaces the green colour of the yolk, becoming, however, paler as invagination proceeds. In the later stages, where the tissues are becoming more transparent, the green-coloured yolk is again seen.

As in *Lepidosiren*, the medullary groove arises far forwards and grows back to the blastopore. In *Protopterus* (Pl. X. fig. 6) the medullary folds, though wider in proportion to the surface of the egg than in *Lepidosiren* (*op. cit.* figs. 17 *h* & 18 *h*), are not quite so definite, but undoubtedly do encircle the blastopore in the same way just before they close. From an external examination the blastopore seems to remain more widely open after closure of the medullary folds than in *Lepidosiren*.

Pl. X. figs. 7 & 8, corresponding with *Lepidosiren* (*op. cit.* figs. 21, 22, & 23), show a very similar origin of the brain, optic outgrowths, branchial and pronephric eminences, but the pair of folds which will subsequently give rise to the mandibular and hyoidean visceral arches is much more marked in *Protopterus* (Pl. X. fig. 7, *M.H.*). The pronephric ducts have also an origin identical with *Lepidosiren* (*op. cit.* figs. 21 *m*, 22 *m*, 23 *m*). In Pl. X. fig. 8, which corresponds very nearly otherwise in development with *Lepidosiren* (*op. cit.* fig. 23 *l*), the whole embryo is not so flattened on the yolk, the head and tail-fold being much more conspicuous. At this stage is seen the first appearance of the crescent-shaped sucker (Pl. X. fig. 8, *c.o.*) first shown in *Lepidosiren* (*op. cit.* fig. 24).

In *Lepidosiren* the branchial arches arise on either side, first as one eminence (*op. cit.* fig. 22), later three eminences (fig. 23); the last of these then splits into two, and thus the four arches are formed. In *Protopterus* they arise first as one eminence (Pl. X. fig. 7, *br.*); later two eminences (Pl. X. fig. 8, *br.* I. & II., *br.* III. & IV.), these then each split into two[1] (Pl. X. fig. 9, *br.* I. II. III. IV.), thus giving rise to the four branchial arches.

In *Protopterus* (Pl. X. fig. 9, *M.H.*), anterior to the four branchial arches, there may be seen an indication of the mandibular and hyoidean arches, which in *Lepidosiren* (*op. cit.* fig. 24) are represented by a single eminence.

Protopterus hatches about the stage of Pl. X. fig. 10, often a little later, in some cases as late as Pl. X. fig. 11. Before hatching there appears to be a covering of cilia, for particles in the fluid within the egg-capsule stream down the sides of the embryo towards the tail end. At hatching the four pairs of external gills are a good deal in advance of the gills of *Lepidosiren*, the developing pinnæ being clearly seen. The rate and direction of growth of the first pair of external gills is very different to that of

[1] The cleavage of the hindermost eminence to form the 3rd and 4th branchial arches occurs somewhat later than that of the foremost eminence.

the succeeding pairs as shown in Pl. X. figs. 10 & 11, *Eg.* I. Here also may be seen, through the dorsal wall, the auditory cavities and the now large fourth ventricle.

Just before the stage of Pl. X. fig. 12 is reached, pigment begins to appear first in the retina, then on the surface of the head. The fin-folds of the tail now begin to grow rapidly, and attain a much greater size than in *Lepidosiren* (*op. cit.* figs. 31, 32, & 33). A copious network of blood-vessels spreads over the yolk. The sucker is fully functional, and the larvæ hang vertically from the sides of the nest or vessel in which they may be confined. Although in *Lepidosiren* this organ is more conspicuous, yet the larvæ appear only to use it for clinging to the uppermost layer of débris in the nest, and so prevent their falling downwards and getting smothered [1].

A striking feature of *Protopterus* at this stage, compared with *Lepidosiren* (*op. cit.* figs. 31, 32), is the serial arrangement of the external gills, their roots being distinct from one another, and placed in a line along the dorsal surface of the deepest part of the yolk. Anterior to the first branchial cleft there is a faint indication of a spiracular cleft between the mandibular and the hyoidean arches (Pl. X. fig. 12, *sp.*) of which in *Lepidosiren*, externally at least, there is no trace.

The roots of the external gills in *Protopterus* (Pl. X. fig. 13) remain longer separated from one another than in the *Lepidosiren* (*op. cit.* fig. 33). The three posterior pairs also attain a greater proportionate size. At this stage the tail and dorsal fin-fold are considerably more developed than in the corresponding stage of *Lepidosiren*.

As the external gills are reaching their maximum development, the origin of the gills become somewhat concentrated and rotate forwards, the hindermost gill becoming dorsal, the anterior becoming ventral.

For some days before leaving the nest, when the young larvæ are hanging suspended vertically from its walls by their suckers, the external gills are held stiffly out at right angles to the axis of the body, forming a radiating frill around the base of the head. When the larva is lying in a small trough of water, the gills are not thus erected, and as the drawing (Pl. X. fig. 13) was taken from a living specimen, the gills are shown lying back along the sides of the body.

The pectoral and pelvic limbs develop synchronously as in *Lepidosiren*, and are just beginning to bud in Pl. X. fig. 12, *h.l.* Correlated with the extension backwards of the roots of the external gills, the position of the bud of the pectoral fin is also far back, and lying immediately below the last external gill, is hidden by them. In Pl. X. fig. 13 the pectoral limbs are of about the same size as the shafts of the external gills. In one case a specimen had not developed the pinnæ of one external gill. This bare shaft so much resembled the pectoral limb, that the larva appeared to have two pectoral limbs on one side.

In Pl. X. fig. 13 the operculum is growing back, the mouth is open, and the internal gills functional. The larvæ do not breathe air before leaving the nest. There is now a considerable development of pigment, especially in the anterior dorsal part of the

[1] Kerr, *loc. cit.* p. 316.

body. The fin-rays are just making their appearance in the fin-folds of the tail. The sucker or cement-organ is at its maximum development. The tail is absolutely diphycercal from the first. Blood-vessels running in the track of the spiral valve shine through the body-wall (Pl. X. fig. 12, *s.v.g.*). The spiral valve is first indicated in fig. 12. The yolk remains chiefly massed in the original position close behind the sucker, and is not distributed along the gut to the same extent as in *Lepidosiren* (*op. cit.* figs. 33, 34, & 35). Wherever yolk is seen, it is of the original greenish colour.

The young *Protopterus* leaves the nest with practically the form of the adult (Pl. XI. fig. 3). The mass of food-yolk is not entirely absorbed as yet. The first pair of external gills has been lost, and the succeeding pairs have been much reduced in size. The tail ends in a very fine filament. The markings of the young *Protopterus* at this time are somewhat different from the adult. The general colour is dark brown, a conspicuous broad yellow band passing between the eyes. As with *Lepidosiren* so with *Protopterus*, the larvæ at this stage contract their black chromatophores at night and become blood-red, the eye shining out deep black in contrast.

It is here interesting to notice that the larval *Protopteri*, after leaving the nest when kept in an aquarium the bottom of which was covered with seedling water-lilies, chara, &c., never show themselves by day, and if disturbed from their seclusion, hastily make their way back to their hiding-place. After dark, however, by the aid of a lantern, the larvæ may be seen swimming around in the most lively manner, but they do not come to the surface for air.

It seems, then, that the habit of expanding the chromatophores by day is of advantage to the larval *Protopterus*, making it almost invisible while lying passively on the dark soil. The chromatophores become contracted by night, not by reason of the darkness, but because this is the period of activity with the larvæ, and when swimming about they are certainly less conspicuous when transparent than when opaque, even at night.

Were it customary for the larval *Protopterus* to swim about in the daytime, they would probably then contract their chromatophores, becoming less visible with increased transparency. As a matter of fact, when in the daylight the larvæ were placed in a white porcelain dish, in a large number of cases they did contract their chromatophores. That this contraction on a light background did not always take place may possibly be accounted for by supposing that continued habit has produced a certain periodicity in the contraction and expansion of the chromatophores.

While on the Gambia, I kept a large number of young fry of about fifteen species of fishes, and I noticed that the nocturnal forms did become more transparent at night. The converse was naturally not noticed, since I know of no fishes which are only active in the daytime. With frogs, the case is quite different, for they are not aquatic, and would not therefore be made less conspicuous by being transparent. The chromatophores are often contracted by them in the daytime when exposed to strong sunlight, for the objects around them then become of brighter and lighter colour [1].

[1] "Notes on the Batrachians of the Paraguayan Chaco," Q. J. M. S. 1899, pp. 314, 327, 328.

Soon after leaving the nest, the larvæ begin to feed on almost any animal matter they can get. For this reason, though I started homewards with a number of larvæ taken from the nest, only one reached England alive, having eaten all the others. On the voyage home, the young *Protopterus* began to move about in the daytime, ceased becoming transparent at night, lost the external gills, all but small vestiges, and began to come to the surface for air. This was about one month after leaving the nest, or about seven weeks after being laid. On reaching England it had quite the form of the adult.

In comparing the development of *Protopterus* with that of *Lepidosiren*, a very noticeable circumstance is the impossibility of comparing together a larva of each form as being exactly at the same stage of development. The various organs and features do not make their appearance in quite the same proportionate periods of time in the two forms; so that at any one stage, some set of organs in the one will not correspond in its state of development with the same set in the other.

Many of the differences noted in the external development of the two forms may, I think, be correlated with the presence in *Lepidosiren* of rather more food-yolk. The main differences are:—

1. A more complete separation in *Protopterus* of the cleavage-products.
2. The greater size of the medullary folds.
3. A more distinct remnant of the blastopore.
4. The earlier appearance of the cement-organ.
5. The earlier rising-up of the embryo off the yolk.
6. The appearance of two visceral folds in front of the four branchial folds.
7. A rudiment of a cleft between them.
8. The greater size of the gills at hatching.
9. The more complete separation of the external gills.
10. The rotation forwards of the external gills.
11. The concentration of the yolk forwards.

I have not thought it well to make any observations upon the bearings of the facts here described, since it is first necessary to know more of the development than can be learnt from a superficial examination. Mr. Graham Kerr has undertaken to further study the development of *Protopterus* and to incorporate the results in his work on the development of *Lepidosiren*. I have here described the external features in development together with what I observed of the nesting-habits of *Protopterus*, as it would be difficult to treat either separately.

Comparing the nesting-habits of *Protopterus* with those of *Lepidosiren*, perhaps the most striking difference is the development by the male *Lepidosiren* in the breeding-season of the extraordinary vascular fringes of the pelvic fins, recently described by Kerr. Nothing of the kind is developed by *Protopterus*. Now, looking to the solution of the problem as to what is the function of these fringes in *Lepidosiren*, it is natural to look to see in what the habits of the latter differ from those of *Protopterus*.

The most striking difference is surely that, whereas *Lepidosiren* makes its nest several feet below the surface of the water, *Protopterus* makes its nest practically out of the water. I regard the habit of *Protopterus* of lashing the surface of the water at the entrance to its nest as a means of aerating the eggs in the nest. Now, it is tempting to regard the vascular fringes on the pelvic limbs of *Lepidosiren* as in some way connected with the aeration of the eggs, for it is obviously unable to make use of this method of aeration adopted by *Protopterus*. But the conditions under which this habit was observed in *Protopterus* were, as I have said, somewhat unusual, in that, owing to prolonged drought, the water in the nest was unconnected with the surrounding water. When this was not the case, the lashing of the tail on the surface of the water was not observed. Therefore I do not think this habit can be said to be quite characteristic of *Protopterus*. The entrances to the nests, however, were always only a few inches at most below the surface of the water, while with *Lepidosiren* the nests are made in deep water, and it seems more probable that the fringes on the pelvic limbs of *Lepidosiren* are, as Kerr holds, accessory organs of respiration avoiding the necessity of frequent absence from the nest in order to visit the surface for air, and thus perhaps risking loss of the entrance to the nest or the attacks of enemies. *Protopterus*, by reason of the shallowness of the water about the entrance to the nest, would not run these risks in seeking air, and therefore has no need of the accessory breathing-apparatus.

IV.—The Nesting-habits of *Gymnarchus*.

While hunting for *Polypterus* eggs, I met with several large floating nests measuring in all two feet in length and one in breadth. The nests were made in the dense grasses of the swamp in three to four feet of water (text-fig. 20). The inside measurement was about a foot by six inches. Three sides of the nest projected from the water; the fourth side was several inches lower, being about two inches below surface. The deepest part of the nest was opposite to that side where the wall was low, the bottom being about six inches below the surface of the water.

In this nest were deposited about a thousand large spherical amber-like eggs 10 mm. in diameter. The eggs hatched five days after being laid, and in eighteen days a thousand young fry of *Gymnarchus niloticus* left the nest when three inches long. This fish is called by the natives the "Suyo."

Though there are many interesting features in the development of these eggs, I do not intend to deal with them in detail here, but merely to mention that the development is exceedingly shark-like. The larvæ soon after hatching develop extremely long gill-filaments, which hang down in two blood-red branches from the gill-arches, of which there are four. The yolk-sac, at first spherical, later becomes drawn out into a long cylindrical bag, attached somewhat far behind for a Teleostean, and covered with a vascular network (Pl. XI. figs. 4 & 5).

The tail is from first to last perfectly diphycercal, and is at first provided with a dorsal and a ventral fin-fold reaching right to the tip of the tail.

Before leaving the nest, both outer gill-filaments and yolk-sac are absorbed and the mature form is reached.

Immediately after hatching, the larvæ commence their characteristic movements, throwing the head and fore part of the body from side to side incessantly. The larvæ are at first so small in proportion to the size of the yolk-sac, that they are quite unable to move it. By this constant movement the larvæ tend towards the surface, and the

Text-fig. 20.

Floating nest of *Gymnarchus*.

weight of the yolk tending downwards, the yolk-sac becomes gradually drawn out into the long appendage already mentioned. About three days after hatching, the larvæ are strong enough by their movements to raise the yolk-sac off the bottom of the nest for a moment, but it is quickly drawn back by its weight.

By the tenth day after hatching, the larvæ are able to drag their yolk-sac to the surface of the water, when they take a gulp of air into their lung-like swim-bladder and fall again to the bottom, on reaching which they again start for the surface with unceasing regularity, so that when looked at from above the nest of *Gymnarchus*, with its swarm of scarlet-bearded, yolk-hampered larvæ, presents a most amazing spectacle.

By the time the huge yolk-sac has been completely absorbed, the young larvæ are ready to leave the nest. They still, however, continue their ceaseless journeyings to the surface for air. It may now be noticed, however, that the passage back to the bottom of the nest is not merely a passive falling, but that the young larvæ actually dart backwards from the surface. When the young *Gymnarchus* leaves the nest it has fully developed the characteristic cylindrical tail of the adult, and in this connection its habits are very interesting.

The *Gymnarchus* propels itself through the water, not by the action of its paired fins, not by the motion of its tail or the undulatory motion of the axis of its body, but entirely by the action of its dorsal fin. This fin extends nearly the whole length of the dorsal surface, ceasing abruptly at the commencement of the cylindrical tail. When *Gymnarchus* starts forwards, the motion is the result of a series of waves passing backwards along the dorsal fin. About five such waves are passing at a time. Suddenly the fish will proceed at the same rate in the opposite direction, and now the motion is the result of a series of waves passing forwards along the dorsal fin.

As the *Gymnarchus* swims rapidly backwards in this way, it may be seen to guide itself through the grasses by using this peculiar tail which it possesses as a feeler. Thus it appears to be quite immaterial to the fish which way it progresses, and it always appears to swim in comparatively straight lines.

How *Gymnarchus* constructs the wonderful floating nest in which it lays its eggs I have been unable to observe. The natives approach these nests with great caution, stating that the parent is at this time extremely fierce and has a very formidable bite. Both the adult fish and its eggs are greatly sought after as food.

A large number of the young fry of *Gymnarchus*, which I had caught immediately they left the nest, lived well on chopped-up worms. I tried to bring some of them to England alive, but every one died as we got into colder climes.

V.—The Nesting-habits of *Heterotis niloticus* Cuv.

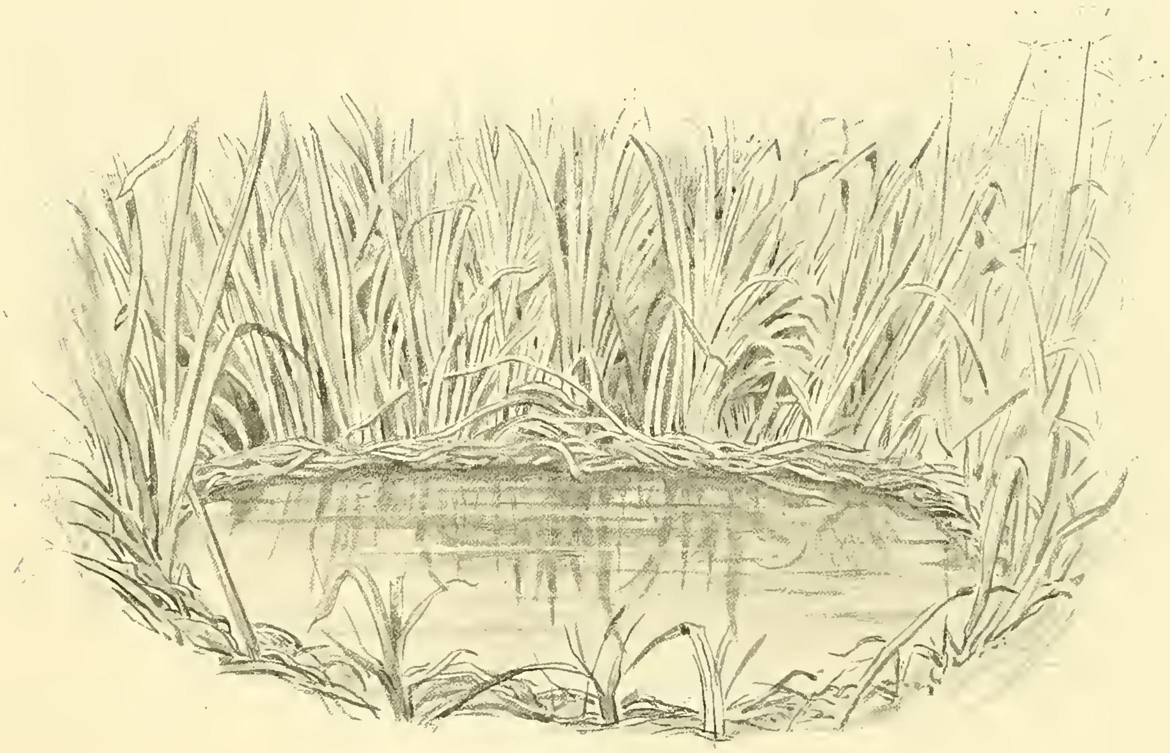
In the same swamps, during the month of July, a most striking feature is the presence of numbers of enormous nests, which proved to be those of *Heterotis niloticus* (text-fig. 21). These nests measured four feet in diameter, and were made in about two feet of water. In wading through the reed-choked swamp, when one came across one of these structures they appeared like miniature lagoons. The walls of the nest were about eight inches thick at the top and compact, being made of the stems of the grasses removed by the fish from the centre of the nest. The floor of the nest was the swamp-bottom, and was made perfectly smooth and bare.

Once I watched a "Fantang," as the natives call this fish, making its nest. It was circling round and round the wall of its nest, every now and then throwing its tail upwards and outwards, tossing on to the top of the wall the débris from the inside of the nest. Thus it toiled on until the wall reached the surface of the water and was complete. When the nest was finished, the water it contained was perfectly clean and clear, so that I could see with my water-telescope the eggs nearly covering the bottom of the nest. When all the eggs are laid, the fish leaves the nest by a hole at one side.

The eggs, which measure $2\frac{1}{2}$ mm., then appear to hatch in about two days, though, owing to the distance the nests were from my quarters, of this I am not certain. The nest appears to be used for at most four or five days. As soon as the larvæ are hatched, they begin to strike up from the bottom. The day after hatching they may be seen continually passing up and down, and are now provided with long external gill-filaments of a blood-red colour, but not so numerous or so long as in the case of *Gymnarchus* (Pl. XI. fig. 6 & 7).

The following day they cease to pass up and down, and converging to a swarm about one foot in diameter, form a deep continuous circle remarkable for its regularity and

Text-fig. 21.



Nest of *Heterotis*.

persistence. The swarm occupies the exact centre of the little lagoon. The young fry, which by now have lost the long external gill-filaments, are seen to be steadily careering round and round ever in the same direction for at least a day. About the fourth day the swarm becomes less persistent and regular, the larvæ swimming first to one side of the nest and then to the other, until about the fifth day they leave the nest by the exit for a few trial trips attended by the parent, and finally leave it altogether, swimming hither and thither in a dense swarm, from which the parent is never far distant. I kept a large number of the young fry for several weeks, but could not get them to feed, and eventually they all died.

The ova of *Heterotis* are shed into the cœlom as in the Salmon. *Heterotis* belongs to the group Osteoglossidæ, which has much the same distribution as the Dipnoi, though it seems doubtful whether this points to an antiquity of the group equal to that of the Dipnoi. Günther, however, regards the Osteoglossidæ as one of the earliest types of Teleostean fishes.

VI.—The Nesting-habits of *Sarcodaces odoë* Bl.

In these same flooded grass-lands the eye is frequently caught by masses of whi t foam floating on the surface of the water. On close inspection it is seen to be filled with numerous transparent ova, about the same size as those of *Heterotis* ($2\frac{1}{2}$ mm.). Soon these eggs hatch, and on hatching make their way through the foam, in which they are laid, down to the surface of the water, and there the young larvæ hang holding to the surface of the water by a large adhesive organ situated on the front of the head (Pl. XI. fig. 8 & 9, *c.o.*).

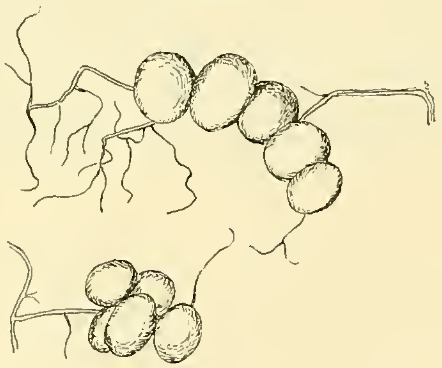
The natives assured me that these were the eggs of the Sannko, more scientifically *Sarcodaces odoë*. On rearing some of these larvæ, I was able to confirm this statement.

Sarcodaces is one of the *Characinidæ*, of which family examples occur in Africa and South America.

VII.—The Nesting-habits of *Hyperopisus bebe* Lacép.

It was a curious fact that of the six species of *Mormyridæ* which I obtained in the Gambia, only one besides *Gymnarchus* was found breeding in the swamps. This was *Hyperopisus bebe* Lacép.

Text-fig. 22.

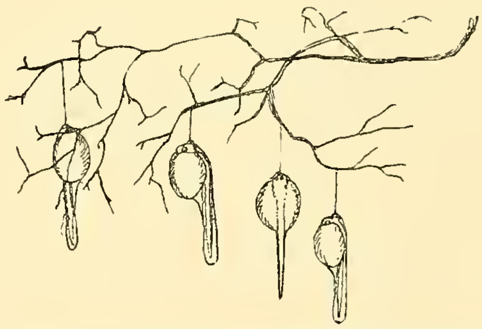


Eggs from nest, supposed to be that of *Hyperopisus bebe.*

Although I did not succeed in finding fertilized eggs of *Hyperopisus* this year, I obtained a number of females full of ripe eggs. I am practically certain that these ovarian eggs are identical with the eggs which I studied last year under the impression that they were the eggs of *Polypterus*.

These eggs were laid in shallow depressions of the swamp bottom, and attached to the rootlets of the grasses laid bare by the parent in scooping out the depression for the reception of the eggs (text-fig. 22, p. 130). The eggs are very small, about $1\frac{1}{4}$ mm. in diameter, and slightly oval, the long axis being rather over $1\frac{1}{4}$ mm. in length. They are yellowish in colour and semitransparent. The eggs hatch in four days, and are then provided with four large cement-glands situated on the top of the head, and two smaller ones on the front of the head (Pl. XI. fig. 10, *c.o.*). Immediately the larva is hatched it runs the upper part of its head against the rootlets, and wriggling away again, draws out from the four cement-glands four fine threads of viscid mucus, which are hardened by contact with the water, and form a minute rope about the length of the body of the larva. By this the larva hangs suspended for four or five days until the yolk is absorbed. If the larva is detached meanwhile, a fresh rope is formed by a fresh secretion of mucus (text-fig. 23). While hanging thus, each larva continually oscillates the whole length of its body from side to side. In one nest there are many thousands of these larvæ suspended

Text-fig. 23.



Larvæ, supposed to be those of *Hyperopisus bebe*, suspended from the rootlets in the nest.

in this way, presenting the appearance of a shaking mass of jelly, for all the larvæ oscillate themselves in unison. I was unfortunately unable to rear any of these larvæ to a stage old enough to be able to identify them.

VIII.—Conclusion.

I should here state that I had great difficulty in keeping alive any of the fish-larvæ that I found for any length of time in any but the natural conditions, *Protopterus*, however, excepted. In the case of *Gymnarchus* a great number of ways was tried, even floating perforated trays as an attempt to imitate the natural conditions. I do not so much wonder at my want of success in this as at the successful way in which the larvæ are hatched out in nature. I never found a dead larva in any nest of *Gymnarchus*, notwithstanding that the eggs and larvæ were lying within six inches of the surface of the water, quite unprotected from the burning rays of a tropical sun and the lashing of the tropical rains. The extremes of temperature taken in the nests were 25° C. and 32°·5 C. But supposing the larvæ to be so constituted that they can withstand the changes of the weather, how is it that large conspicuous eggs in very conspicuous nests on the surface of the water escape forming the food of the abundant bird-life of these swamps?

In the breeding-habits of the last four types I have described, the interesting fact comes out that the first two and the last two each have, in common, organs in the larva which are usually regarded as not belonging to the Teleostean division of fishes. *Gymnarchus* and *Heterotis* have each, for a time, enormously elongated gill-filaments, structures which are so characteristic of Elasmobranch larvæ. Something of the kind was noticed in the development of the loach by Götte[1], but I think this is the only case of such organs in the Teleosteans. *Sarcodaces* and *Hyperopisus* have each well-developed cement-organs on the head. These structures are generally regarded as characteristic of the Ganoids. It seems, then, that the conditions by which fishes, which breed in tropical fresh waters, are surrounded is conducive to the development of very various accessory organs in the larva, both for the purpose of respiration and also of preserving them from harmful contact with their surroundings, and that these structures cannot be regarded as having any great morphological meaning. The resemblance of the embryo of *Gymnarchus* to that of an Elasmobranch I hope to discuss in a future work on the development of *Gymnarchus*.

IX.—EXPLANATION OF THE PLATES.

All the figures of Plate X. were originally drawn by myself with the aid of a camera lucida, and were then copied by Mr. Edwin Wilson.

Figs. 2, 3, 4, 5, 12, & 13 were drawn on the Gambia from living specimens. Figs. 1, 6, 7, 8, 9, 10, & 11 were drawn from formalin specimens.

The magnification is 8 diameters.

The figures in Plate XI. were all drawn by myself except fig. 1, which was from a specimen preserved in formalin, drawn by Mr. Edwin Wilson under my supervision and coloured from my notes by myself. Figs. 4, 5, 6, 7, & 8 were drawn from life on the Gambia. Fig. 3 was drawn from a specimen preserved with corrosive sublimate and acetic acid.

au., auditory sac; *bp.*, blastopore; *br.*, branchial eminences; *br.* I. II. &c., branchial arches; *c.o.*, cement-organ; *cl.*, position of cloaca; *ep.e.*, growing edge of epiblast; *Eg.* I. II. &c., external gills; *f.f.*, dorsal fin-fold; *h.l.*, hind limb; *H.*, hyoid arch; *H.br.*, hyobranchial cleft; *invag.*, line of invagination; *M.*, mandibular arch; *M.H.*, mandibulo-hyoid fold; *m.f.*, medullary folds; *o.c.*, optic outgrowth from brain; *op.*, operculum; *p.f.*, pectoral fin; *pn.*, pronephros; *s.v.g.*, groove marking rudiment of spiral valve; *sp.*, groove between mandibular and hyoid arches; *v.* IV., fourth ventricle; *y.k.*, yolk-cells.

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[1] "Entwick. d. Teleostierkeime," Zool. Anz. No. 3, 1878.

PLATE X.

PLATE X.

The figures of this Plate illustrate the external features in the development of *Protopterus annectens*, Ow.

Fig. 1. Egg on the first day of observation, segmentation somewhat advanced: p. 121.

Fig. 2. Egg on the morning of the second day, showing commencement of invagination: p. 121.

Fig. 3. Egg on the evening of the second day, showing a further stage of invagination. Above is seen a transparent portion indicating the segmentation-cavity: p. 121.

Fig. 3 *a*. A variation of the stage shown in fig. 3. The area of the disappearing yolk-cells is viewed from a somewhat different aspect, in order to show that the line of invagination is not here straight but curved: p. 121.

Fig. 4. Egg on the morning of the third day, showing the straight line of invagination and the gradual disappearance of the large-celled yolk: p. 121.

Fig. 4 *a*. A variation of the stage shown in fig. 4, showing that the line of invagination is not always straight: p. 121.

Fig. 5. Egg on the evening of the third day, showing the last stage of invagination: p. 121.

Fig. 6. Egg on the morning of the fourth day, showing medullary folds encircling the blastopore: p. 122.

Fig. 7. Embryo on the evening of the fourth day, showing origin of optic outgrowths, mandibulo-hyoid fold, branchial eminence, and pronephros: p. 122.

Fig. 8. Embryo on the fifth day, showing the segmentation of the mandibulo-hyoid fold and first segmentation of branchial eminence; also the remnant of the blastopore, and the first appearance of the cement-organ, and the development of the head and tail-folds: p. 122.

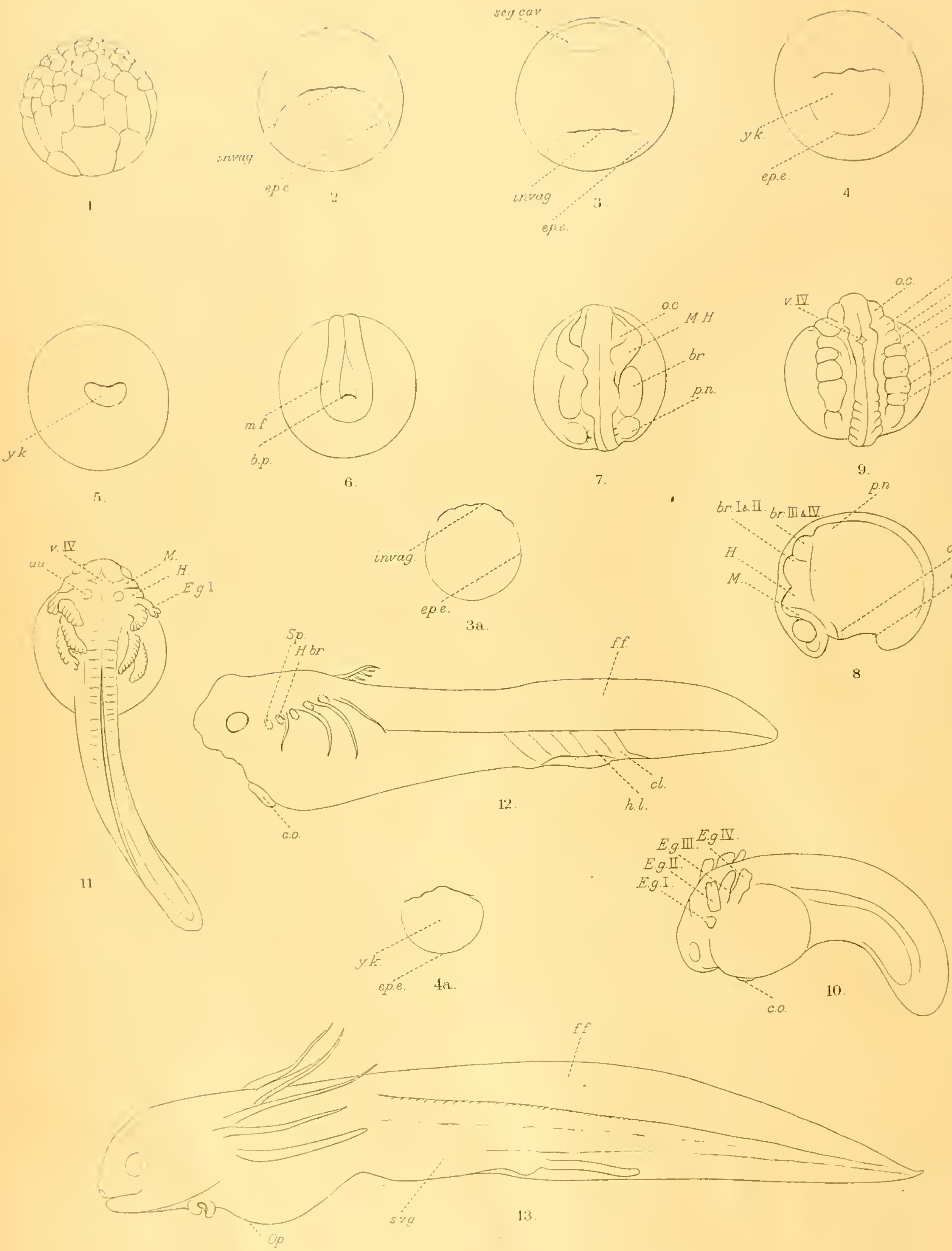
Fig. 9. Embryo on the sixth day, showing the further segmentation of the branchial eminence into four: p. 122.

Fig. 10. Embryo on the seventh day, showing the first pairs of external gills strongly differentiated from the second, third, and fourth pairs. The trunk of the embryo has grown back from the main mass of yolk, taking much of the yolk with it. The true tail is not yet formed: p. 122.

Fig. 11. Larva on the eighth day, just hatched, showing further growth of the external gills, and the auditory sacs showing through the tissues. The true tail-region has now begun to grow: p. 122.

Fig. 12. Larva on the tenth day, showing the serial arrangement of the external gills, the indication of the spiracular cleft, the first trace of the hind limbs, being now anterior to the position of the cloaca, and the well-developed and functional cement-organ. The tail-fins are now well-developed. Pigment has appeared on the head: p. 123.

Fig. 13. Larva on the seventeenth day, showing general advancement, the rotation of the external gill, the operculum, the vessel in the spiral valve groove, and the well-developed limbs: p. 123.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